



CONSERVATION BIOLOGY 00

Large Herbivore Ecology, Ecosystem Dynamics and Conservation

Edited by Kjell Danell, Roger Bergström,
Patrick Duncan and John Pastor



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Large Herbivore Ecology, Ecosystem Dynamics and Conservation

The major drivers forming the shape and function of terrestrial ecosystems are large herbivores. These animals modify primary production, nutrient cycles, soil properties and fire regimes, which all have an impact on the ecology of other organisms. Most large herbivores require some type of management within their habitats, as some species populations are at the brink of extinction, and others already occur in dense populations causing conflicts with other land uses. Due to the huge importance of herbivores in shaping a wide variety of ecosystems worldwide, it is important to understand how and why these communities function the way they do, and what implications this has not only for the conservation of the herbivores themselves but also for the conservation of the habitats as a whole. This book deals with the scientific basis for the management of these systems.

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Conservation Biology

Conservation biology is a flourishing field, but there is still enormous potential for making further use of the science that underpins it. This new series aims to present internationally significant contributions from leading researchers in particularly active areas of conservation biology. It will focus on topics where basic theory is strong and where there are pressing problems for practical conservation. The series will include both single-authored and edited volumes and will adopt a direct and accessible style targeted at interested undergraduates, postgraduates, researchers and university teachers. Books and chapters will be rounded, authoritative accounts of particular areas with the emphasis on review rather than original data papers. The series is the result of a collaboration between the Zoological Society of London and Cambridge University Press. The series editor is Professor Morris Gosling, Professor of Animal Behaviour at the University of Newcastle upon Tyne. The series ethos is that there are unexploited areas of basic science that can help define conservation biology and bring a radical new agenda to the solution of pressing conservation problems.

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Preface

Large herbivores are, and have for a long time been, among the major drivers for forming the shape and function of terrestrial ecosystems. These animals may modify primary production, nutrient cycles, soil properties, fire regimes as well as other biota. Some large herbivore species/populations are at the edge of extinction and great effort is being made to save them. Other species/populations are under discussion for reintroduction. Still other species occur in dense populations and cause conflicts with other land use interests. Overall, most large herbivores need some type of management and, according to our view, these operations should be scientifically based.

There is a great amount of scientific information on large herbivores in different regions of the world. We felt that there was an urgent need to bring this knowledge together and to make it available for a larger public outside the group of specialists. We also felt that synthesis of results from one region may be valuable for scientists working in other regions and with other species.

To initiate a first synthesis of the knowledge on large herbivores we held a workshop on 'The impact of large mammalian herbivores on biodiversity, ecosystem structure and function' 22–26 May 2002 at Kronlund outside Umeå in northern Sweden. The event brought together scientists from different disciplines and with experience of large herbivore research in different biomes. During the workshop the idea of a book was developed over time and some more specialists were invited to the synthesis.

We thank the financial support given by Swedish Environmental Protection Agency, The Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning, Swedish Association for Hunting and Wildlife Management and the Faculty of Forest Sciences of the Swedish University of Agricultural Sciences. Special thanks are due to the representatives for the forest companies, the hunting organizations, and the

Saami people who gave valuable inputs and stimulated the discussions during the field trip of the workshop.

This book represents the culmination of the process initiated by the workshop. Edited volumes are by definition collaborative efforts. This book would not have been possible without the patience and strong commitment of all the contributors, including the numerous reviewers. We are deeply grateful for their efforts, collaboration and for allotting time and sharing insights and data. Special appreciation is due to Dr Tuulikki Rooke who provided excellent assistance during the last stage of the preparation of the book.

We are fully aware of the fact that this book gives only one perspective of large herbivores – the one seen by natural scientists. We hope that a similar effort will be made by scientists doing research on the human dimension of large herbivores. In concert, we hope these efforts will give valuable insights for managers and scientists, stimulate further studies and make further syntheses possible.

Introduction

PATRICK DUNCAN, KJELL DANELL,
ROGER BERGSTRÖM AND JOHN PASTOR

Biodiversity and productivity vary strongly among ecosystems: understanding the causes of these variations is a primary objective of ecology. To date a few overarching principles have been established. One is the species-area relationship: the species diversity of a system depends principally on its area, and some major mechanisms underlying this principle have been identified (Rosenzweig 1995). The structure and dynamics of plant communities also affect biodiversity profoundly. Edaphic conditions set the bounds for plant communities, and fire can be a key determinant of their structure and diversity. In addition, at least in some ecosystems, large herbivores are 'keystone' species, so the systems have very different structures according to whether large herbivores are present or absent. There is also some evidence that large herbivores affect plant productivity, from modelling (de Mazancourt *et al.* 1998) as well as empirical work (McNaughton 1985).

Understanding the role of large herbivores is therefore important for ecology, and also because the abundance of these animals can have profound effects on the conservation status of other species, through their impact on plant communities. However, the literature on these questions is rather difficult to access especially for people who are not academic ecologists. Reviewing the impact of large herbivores on ecosystems was identified as a priority in the Action Plan for the Large Herbivore Initiative for Europe and Central Asia (see <http://www.largeherbivore.org>). In some areas the ungulate populations are 'overabundant' and have serious negative impacts on forestry, agriculture and biodiversity. In other areas the

ungulate populations are approaching extinction. There are thus many urgent management and conservation problems connected to large herbivores, and an accessible review of existing knowledge is urgently needed to underpin progress towards effective management.

In May 2002 Kjell Danell, Roger Bergström and John Pastor convened a workshop in Sweden to review 'The Impact of Large Mammalian Herbivores on Biodiversity, Ecosystem Structure and Function' and this book is the result of the work that started there. It focuses on wild large herbivores since information on domestic animals is voluminous and easier to access (though it could also benefit from being analysed to answer ecological questions!). Our main aim was to provide an up to date review of existing knowledge on the impact of large herbivores on species richness, ecosystem structure and function in the major habitats of the world. We also explore what is known about the consequences of global change on large herbivores populations, and their impact on ecosystems, and what needs to be done to improve our understanding of this crucial area.

The [first chapter](#), 'Large herbivores across biomes' by H. Fritz and A. Loison, presents the major communities of wild large herbivores in all the continents. For the purposes of this book, we define large herbivores as even-toed (Artiodactyla) and odd-toed ungulates (Perissodactyla) over 5kg, and elephants (Proboscidea). The abundance of large herbivores, at least in Africa at a regional scale, are determined ultimately by the abundance of their resources. The general principles underlying the diversity of their communities in all the continents are reviewed, starting with what is known about their palaeohistory. The patterns of distribution of some of the key life history traits are also reviewed, body size, mating system, sexual dimorphism and litter weight. The different body sizes are distributed across habitats and feeding guilds in log normal (hump-backed) distributions, whose modes increase with openness of the habitats, and this is true for marsupials as well as eutherians. Dimorphism in body mass is closely related to polygyny in Artiodactyla, but not in the other groups, so other variables are clearly important here. Demographic strategies, which also vary considerably, nonetheless show some clear patterns: large herbivores share high and relatively constant adult survival, relatively early and variable age at maturity, and a relatively low and very variable juvenile survival. These patterns appear to hold true across phylogeny, biomes, habitat and feeding types.

The following chapters in the first part of the book deal with determinants of the dynamics of large herbivore populations and communities,

notably the linkage between resource abundance and population dynamics, the capacity of large herbivores to cope with seasonality in resources and in climatic conditions, and the interplay between large herbivores and large predators.

In Chapter 2, **‘Living in a seasonal environment’** by J. Moen, R. Andersen and A.W. Illius, the focus is on a biome where seasonality is extreme, the Arctic. The effects of climatic variability on population sizes are analysed, and then the mechanisms are explored by evaluating the effects of environmental stochasticity on life history tactics of large herbivores (e.g. capital vs. income breeding), and the role of body size. Many models of global change predict an increase in the season of vegetative growth, which is already detectable, and the resulting increase in plant growth will generally be positive for large herbivores as both plant biomass and nutritional quality will increase. The decrease in snow cover (in some areas) will also be positive for large herbivores as they will have a longer period for body growth and an increased survival during the shorter winters. However, it is unclear what effect this will have on population dynamics: if climate change leads to increased animal growth and survival, the animal populations may enter winter at densities too high to be supported by winter resources. These climate changes may even result in lower accessibility of winter forage which could cause declines in calf body weight and survival during winter. Long-term monitoring is clearly essential, and coupled models of plant and animal dynamics like those of Illius and O'Connor (2000) could help to direct management of these systems, which are so sensitive to damage by overgrazing.

In Chapter 3, **‘Linking functional responses and foraging behaviour to population dynamics’** by A.W. Illius, an in depth review is given of what is known about a key interface – the interaction between large herbivores and their food resources. Our knowledge of the underlying principles is reviewed, distinguishing the way consumption rates respond to food abundance (i.e. the functional response) from the way the size of the consumer population responds to variations in food consumption (the numerical response). The work of Spalinger and Hobbs (1992) provides a systematic means of analysing functional responses and evaluating biologically meaningful parameters. This is used to review the state of the art in foraging behaviour, diet selection and food intake of wild and domestic herbivores. Andrew Illius concludes by stating ‘there are a priori and empirical grounds for the propositions that optimal patch use is not an appropriate model of resource use by browsing mammalian herbivores, and that longer-term diet optimization, i.e. the trade-off between diet

quality and daily intake rate, is a more likely explanation of their foraging behaviour’.

Approaches to describing how consumer populations change in response to the average per capita food intake are then reviewed, from the simplistic/abstract representations of ecological interactions, such as Lotka-Volterra coupled differential equations to the mechanistic approach of Illius and Gordon (1999). An alternative approach has been developed by Owen-Smith (2002) who describes consumer-resource systems in terms of biomass dynamics, rather than numbers of consumers, and uses aggregated efficiencies of assimilation, metabolism, repair and senescence to model aggregated population dynamics.

In Chapter 4, ‘Impacts of large herbivores on plant community structure and dynamics’ by A.J. Hester, M. Bergman, G.R. Iason and J. Moen, the focus is on the main direct impacts of herbivores on shrub and woodland systems to complement the later reviews, which cover more tree-dominated habitats. Their review covers the effects on individual plants (or ramets) and the range of responses of individual plants to herbivory, as a basis from which to explore the complexities of processes operating at the plant community level. Large herbivores make foraging decisions at a range of spatial (from bite to landscape) and temporal scales (from seconds to years), and plants also respond to herbivore impacts at a similar range of scale (plant part to community). This makes the identification of key processes affecting plant/herbivore interactions and the mechanisms driving plant community responses to herbivores quite a challenge. Some of the apparent controversies in the literature about herbivore influences on vegetation may be due to this difficulty.

Although most direct effects on plants, by grazing or browsing, are negative, indirect effects on seed dispersal, in the gut or on the body, are largely positive. Although some of the seeds do not survive herbivore digestive processes, others require passage through the gut of a herbivore for germination, or at least benefit from it. Further, the effects of large herbivores on seedling establishment are generally positive. Effects of large herbivore activities on plant growth and mortality can of course be strong; these are reviewed in relation to the type of tissue which is affected, the extent and frequency of off-take, and the herbivores involved.

Removal of plant parts above the ground inevitably affects below-ground processes as well. Reallocation of resources, at least in grasses, usually leads to increased shoot growth (i.e. to restoration of root:shoot ratios after damage). Above-ground herbivory can also induce changes in mycorrhizal fungi, thereby affecting nutrient uptake and subsequent

growth and survival. Most studies show declines in mycorrhizal colonization as a result of herbivory, which can have powerful effects on the dynamics of the plant communities.

Plant responses to herbivores are reviewed, including defences (physical and chemical) and tolerance. Plants can avoid large herbivores through their spatial location, visibility (apparency), or by producing defence structures such as thorns, hairs or thick cuticles. They may also produce ‘allelochemicals’; several hypotheses have been proposed to explain their ecological and evolutionary occurrence: the merits of these hypotheses, particularly the ‘carbon-nutrient balance’ hypothesis, are reviewed. The conditions determining ‘tolerance’ and ‘compensation’ are reviewed: although plants are most commonly detrimentally affected by herbivory, there is a long-running debate as there are examples of exact- or overcompensation in a considerable number of studies. Most of these, however, were short-term responses and might not accurately reflect long-term fitness – an important distinction.

There is a wealth of literature on the impact of large herbivores on plant diversity (species, structure and genetic), but still much controversy. This is probably due to both the complexity of the subject and a scarcity of long-term controlled studies where all main driving factors are understood. Most studies indicate that herbivores are more likely to increase the diversity and spatial heterogeneity of plant communities. However, the authors of this chapter show that there are exceptions, and that the conditions under which herbivores increase or decrease diversity and heterogeneity, and the mechanisms involved, are still not fully understood.

Chapter 5, ‘**Long-term effects of herbivory on plant diversity and functional types in arid ecosystems**’ by D. Ward, addresses two contrasting yet widely held beliefs about the dynamics of the vegetation in arid ecosystems: first, that abiotic factors have more impact than biotic factors (principally because herbivores are limited at low densities by sparse resources), so herbivory by mammals is relatively unimportant in ecosystem functioning and biodiversity maintenance, and secondly that heavy grazing has caused land denudation and desertification in semi-arid regions such as the Sahel of Africa. It is important here to distinguish between short-term effects of herbivory (which lead to the removal of phytomass) and long-term ones (which lead to changes in productivity and the species composition of the plant communities). David Ward starts by showing that the results of long-term studies of the effects of large mammals on arid vegetation are not consistent. In some areas the impact

is strong, in others weak. Ward argues that the inconsistency in the results of the long-term studies may result from oscillations of vegetation and herbivore populations: migratory or nomadic movements of the animals could lead to contrasting pressure of herbivory at times of the year, such as the growing season, that are crucial for the dynamics of the plants.

Some of the most interesting effects of herbivory on plant diversity result from the effects of selective herbivory on the relationships among plant functional types, in particular herbaceous vs. woody plants. Ward focuses on the phenomenon of ‘bush encroachment’, as evidence is accumulating that suggests this trend is a general one in arid and semi-arid savannas throughout the world. He illustrates it from arid regions ranging from the Namib and Kalahari deserts, to the Mitchell grass plains of Australia via the southern Sahara, the Negev and central Asian deserts, and reviews the general explanations that have been proposed for bush encroachment. The first is Walter’s two-layer hypothesis, based on tree-grass competition. Later models propose that trees and grasses coexist in a state between that of grassland and forest because the plant communities are ‘pushed back’ into the savanna state by frequent disturbances (human impact, fire, herbivory and drought). Ward then describes the results of experiments to test some of these models, and shows that the results open new perspectives for understanding the fundamental processes and for management of bush encroachment. Under the conventional two-layer competition hypothesis, grazing during years with less than average precipitation should be reduced to a minimum so as not to give the trees a competitive advantage. By contrast, the new results suggest that bush encroachment may not occur when water is limited and consequently such a management protocol would be futile.

Grazing responses in arid and semi-arid rangelands in winter rainfall regions differ from those in summer rainfall regions, and plant height may be a more important factor than palatability, life history or taxonomic affiliation in determining responses to herbivory. Ward argues that the ‘classical’ theory of grassland response to grazing which defines plants as increasers or decreasers has some value in explaining plant responses, but should be replaced by a theory which considers plant size and other relevant traits such as palatability and specific leaf area. More studies on more continents are also needed to tease apart the effects of evolutionary history of grazing and abiotic environmental factors on grazing responses and plant functional traits.

Chapter 6, ‘**The influence of large herbivores on tree recruitment and forest dynamics**’ by R. Gill, shows that the effects of large herbivores

on tree regeneration can be grouped broadly into two main types. Firstly, the effects of feeding on seeds, seedlings and bark, which are damaging, and delay forest succession or accelerate senescence. Secondly, the effects which promote regeneration and thus tend to advance forest succession. There appear to be at least four mechanisms involved in this latter group: regeneration may be promoted through seed dispersal, protection from thorny plants, reduced competition, or, lastly, by reduced fire frequency or fire temperatures as a result of reduced fuel. In general, the retarding effects of herbivory appear to be more prevalent in woodlands and forests, whereas facilitation is more likely to occur in open habitats. The fact that these two contrasting processes occur in different communities has led to the suggestion that large herbivores cause a cycle of succession, where the serial stages of open ground, young trees, maturing woodlands and senescent stands finally give way to open ground again. Large herbivores can therefore create more dynamic woodlands, where changes in tree cover occur continually, and where light-demanding species are favoured at the expense of shade-tolerant ones.

There is evidence for the simultaneous existence of all stages of this cycle, and there is no reason to suggest that the rates of regeneration and senescence will be balanced. Rates of tree regeneration and damage by large herbivores can be highly variable. Facilitation by thorny plants will depend on the suitability of the site for the nurse species. Each species of herbivore has a unique pattern of habitat and diet selection. As a result, the impact of large herbivores can lead to dominance of either grassland or of closed-canopy woodland. The effect of large herbivores on nutrient flows can bring about enduring changes in vegetation composition. Since the amount of food for herbivores can be sharply reduced by shade, animal populations will decline if trees grow dense enough to form closed-canopy woodland over an extensive areas, which then limits the extent to which herbivores can maintain openings. In the savanna regions of Africa, switching between woodland and grassland states can occur: as a result of a combination of grazing, elephants and fire, woodlands in the Serengeti-Mara region were opened up in the 1960s, but began to recover again in part of the region during the 1980s, when elephant numbers were severely reduced. These changes suggest that savanna ecosystems may be unstable, or have alternative stable states, and events affecting herbivore numbers or grazing pressure can prompt major changes in vegetation structure.

Evidence from exclosures suggests that the selective browsing by deer tends to reduce tree species diversity. Unfortunately there is insufficient

information to generalize for other herbivores in forest habitats, although a study of the impact of elephants found that diversity of trees and shrubs were reduced, but diversity of plants near ground level was increased. A similar result was reported for moose browsing, where diversity of the smallest trees increased, but apparently not in older trees.

In Chapter 7, **‘Large herbivores: missing partners of western European light-demanding tree and shrub species?’** by F.W.M. Vera, E.S. Bakker and H. Olff, the consequences of the presence of large herbivores for the vegetation and other biota are addressed. A major criterion for the selection of sites for the conservation of nature in western Europe has always been ‘naturalness’. Curiously there has been little effort to analyse what the natural landscapes looked like. It has often been claimed that temperate Europe without human influence would have been almost entirely covered with a closed canopy broad-leaved forest, the ‘classical’ forest theory. However, these forests contained indigenous species of large herbivores (aurochs, tarpan, red deer, moose, roe deer and European bison). These animals were assumed not to have had a substantial influence on the forest, but to follow the development in the vegetation. Vera *et al.* reviews knowledge from a wide range of disciplines, including palaeontology, palynology, evolutionary ecology, and history, and presents a provocative point of view of the role of large herbivores in temperate forests. They suggest that large herbivores were in fact very important influences on natural temperate forests, and created a park-like landscape over much of temperate Europe with bulk grazers like cattle and horse playing key roles in the processes involved.

These ‘wood pastures’ have an extremely high diversity of plant and animal species, because of the structural diversity of the vegetation. The oak has a special place as a host for insects, since no other species of tree is associated with so many species of insects: more than 50% of all insect species found in Great Britain live in the 20 000 hectares of wood pasture in the New Forest alone, and this landscape is habitat for a great variety of bird species, especially songbirds. These observations are clearly highly relevant to current issues of nature management, at the reserve and the landscape scales.

In Chapter 8, **‘Frugivory in large mammalian herbivores’** by R. Bodmer and D. Ward, the focus is changed to tropical and arid regions. On the basis of a survey of 178 large herbivores species in tropical regions, the occurrence of frugivory is described across the range of stomach complexity in large herbivores, from simple to advanced, and in animals with different adaptations to seed predation, including strengthened jaws,

elaborate dentition and digestive systems. The occurrence of frugivory is compared between tropical forest and savannas, and across the range of body mass in large herbivores. Biomass density (kg km^{-2}) of large herbivores with different diets is compared across habitat types. The impact of frugivores on ecosystem dynamics is a consequence of both seed dispersal and seed predation: the importance of frugivory by mammals in the dynamics of ecosystems is difficult to assess because most of the studies lack detail, and very few measure the vital rates of the tree populations. These issues are illustrated by case studies in two extreme habitats, tropical rainforests and the Negev desert. Resource use by four species of Amazon ungulates in north-eastern Peru is compared using both stomach and faecal samples. The striking differences between the ungulate species are discussed in relation to the physical characteristics of the seeds and the adaptations of the large herbivores.

Work in the Negev on the ecologically important and complex interaction between Acacia trees, bruchid beetles and ungulates (which are both important seed predators) shows that, as expected, when ungulates are present, seed dispersal increases, thus reducing competition for the seedlings from the parent trees. However, contrary to the idea that large mammalian herbivores reduce the impact of seed predation by consuming seed pods before they can be infested, the results of this study indicate that ungulate activity does not reduce the impact of the bruchid beetles on seeds. Very few seeds eaten by bruchids germinate, and many eaten by ungulates do: interestingly the germination rate of Acacia seeds eaten by herbivores increases with the body size of the herbivores. The dispersal of Acacia seeds by large mammalian herbivores seems to have affected and, perhaps controls, the distribution of different ecotypes of Acacia trees on a large geographic scale in the Middle East. In conclusion, browsing by ungulates at high densities, reduced the growth rates of the young Acacia, but did not inhibit juvenile Acacia escaping above the browsing level. Negative effects of browsing on juvenile trees may not translate into changes in tree demography because of the enhancement of seed viability and germination by mammalian herbivores.

Chapter 9, '**Large herbivores as sources of disturbance in ecosystems**' by N. Thompson Hobbs, suggests that herbivores might be profitably viewed as agents of disturbance, or events which alter resource availability or substrates, thereby causing abrupt changes in states and rates of processes. Trampling is an unavoidable disturbance of large herbivores since a large body mass is supported on four hooves, creating a large force per unit area on ground vegetation and soil. Trampling area increases

allometrically with body mass, but so does home range. Population density therefore decreases allometrically with body mass, effectively cancelling any relationship between body mass and the proportion of home range trampled, which is fairly uniform at approximately 7% of the home range trampled each year. But, notes Hobbs, if proportionally more time is spent in certain communities with a small area, then trampling is concentrated in those communities and can affect up to 50% of the area which is actually grazed. This explains the often highly trampled condition around water holes, for example. The effects of trampling are diverse. On the one hand, trampling compacts the soil and reduces water infiltration, but if the soil surface is covered with a biotic crust, as is often the case in arid environments, then trampling increases water infiltration by breaking the crust. Bare, trampled areas are available for colonization by seeds which require exposure to mineral soil, creating a matrix for high, small-scale plant species diversity. Trampling also fragments litter leading to faster decay. Finally, trampled areas are often sites of high colonization by nitrogen (N) fixing cyanobacteria.

Patches of faeces and urine can also be viewed as disturbances since they represent very abrupt changes in nutrient availability from the surrounding areas, a point which echoes that made by Frank in Chapter II. Approximately 2% of an animal's home range is in urine patches at any one time, but if the animal urinates in certain types of sites more often than at random, then, like trampling, the proportion of actually grazed area affected by urination is much higher than expected at random. Hobbs presents equations demonstrating that faecal N deposition increases linearly with plant N concentration and body mass while urine N deposition increases quadratically with body mass and plant N. Therefore, very large herbivores which graze high N forage will return most of their N to the soil as urine, which is more readily available to plants than faecal material since the latter needs to be decomposed by soil microflora. This in turn results in higher plant N, higher productivity, and a higher probability that the herbivore will subsequently graze the urine patch and surrounding area.

Herbivores also modify the occurrence of other disturbances, most notably fire, by reducing standing fuels of dead straw, thereby reducing fire frequency. Herbivores also selectively forage in burned areas of grasslands because of the higher N availability in grass after a burn, and so herbivores can also increase the recurrence interval between fires on a site as well. However, browsers in forested areas tend to avoid plants which produce resinous tissues with high content of volatiles. Since these plant

tissues are of high flammability, large herbivores increase the proportion of flammable species in forests and could possibly increase fire frequency.

In Chapter 10, **'The roles of large herbivores in ecosystem nutrient cycles'** by J.P. Pastor, Y. Cohen and N. Thompson Hobbs, the specific mechanisms by which herbivores affect the rate of nutrient cycling is discussed, using the Serengeti grasslands and the boreal forests as case studies where large herbivores have opposite effects. The herds of large herbivore grazers in the Serengeti increase rates of nitrogen cycling and productivity through deposition of faecal and urinary N. However, in boreal regions, ungulate browsers forage preferentially on tree species whose tissues are more digestible because they have low lignin and high N contents. Conversely, they often avoid conifers with tissues of high lignin and low N contents which decrease their digestibility. Over time, the browsed species are outcompeted by the unbrowsed species, whose litter comes to dominate inputs of N to the soil. The decay of these litters from unbrowsed species is slow because the same chemical properties which make them difficult to digest by the gut flora of the ruminant ungulates also slow decay by soil microflora. Therefore, in the long run selective browsing by ruminant ungulates in boreal regions decreases N cycling and productivity, exactly the opposite response to grazers in grasslands. Using equations presented by Hobbs in the previous chapter, Pastor *et al.* show that there is a critical plant N concentration, above which excretion is mainly as urea, which is readily available for plant uptake, and below which excretion is mainly as faecal material, which is less and less decomposable the lower the N concentration in the original forage. This critical N concentration is in the neighbourhood of 1.5% N, which is the lowest N concentration in the green graminoid forage consumed by grazers but the highest N concentration in twigs consumed by browsers. Pastor *et al.* suggest that positive feedbacks between the large herbivore, plant community and plant tissue chemistry, and soil nitrogen mineralization rates effectively cause divergence to either side of this critical level of plant N, leading to the difference between browsing- and grazing-dominated nutrient cycling regimes shown in the two case studies.

These positive feedbacks between herbivores, plant communities and soils have some interesting implications for the coevolution and conservation of herbivore-dominated ecosystems. Evolutionary stability is possible only when the herbivores increase nutrient cycling rates, as in the Serengeti. When the herbivore decreases nutrient cycling rates, as in boreal forests, the system is subject to invasion by another herbivore species which can reverse the process, and hence the system is not stable.

Conservation policies must also recognize the importance of these feedbacks which could move the system into unwanted states within a few decades or even years.

In Chapter 11, **'Large herbivores in heterogeneous grassland ecosystems'** by D.A. Frank, it is discussed how ungulate decisions in grasslands relate to and change the spatial heterogeneity of food distribution over the seasonal home range, across portions of the landscape, and within a plant community. Ungulates in grasslands make a hierarchy of decisions, from where to move to seasonally across the home range, to which portions of a landscape to graze in within a season, and what plant or plant part to eat locally. All of these decisions are spatial because food is not distributed homogeneously. But the actions of the herbivores resulting from these decisions also affect the future spatial distribution of its food and therefore the future decisions the herbivore and its offspring must make.

Using the grasslands in Yellowstone National Park as an example, Frank shows that as much as 2 kg N per ha per year is moved by ungulates from their summer range at higher elevations to the winter range at lower elevations in carcasses, faeces and urine. This is substantial because it equals N inputs in precipitation; it also amounts to one-fifth to two-thirds of the N in above-ground green forage, a large proportion of annual plant uptake. Within the winter range, ungulates remain on a site in proportion to its productivity rather than its area. While feeding there, they defecate and urinate. Therefore, productive sites get fertilized proportionally more by the ungulates, further increasing their productivity and the contrast between their productivity and that of adjacent less productive sites. Even within a site, urine patches have obviously greener vegetation and are grazed at a higher rate than surrounding patches – up to 14% of the N consumed by an ungulate can come from urine patches. This sets up a positive feedback of nutrient transport to the winter range followed by selecting productive spots, fertilizing those spots, followed by enhanced feeding at those spots. Nitrogen is the nutrient which has the strongest limiting effect on grassland plant species and therefore is the nutrient with most influence on the outcome of competition. The enhanced N availability decreases competition between plant species, thereby promoting coexistence between plant species which can in turn supply a diverse diet. Therefore by concentrating nutrients in the most productive sites, ungulates in grasslands enhance spatial variability but also enhance productivity where they feed the most.

In Chapter 12 **'Modelling of large herbivore-vegetation interactions in a landscape context'** by P.J. Weisberg, M.B. Coughenour and H. Bugmann,

the different modelling approaches for representing large herbivore-landscape interactions are reviewed. They characterize three general approaches: animal-focused, plant-focused, and integrated. The first two approaches are discussed briefly, and the remainder of the chapter focuses on integrated, spatially explicit models which become particularly valuable where research questions involve long time scales over which feedbacks between plant and animal components cannot reasonably be ignored.

Representing the critical, long-term interactions between large herbivores and vegetation requires that vegetation pattern and dynamics be linked to the landscape variability which actually influences large herbivore movement, foraging and distribution. A further problem is that linking large herbivore movements, habitat use, and ultimately population dynamics with landscape pattern requires a multi-scale approach. The authors propose that there is a fundamental mismatch (from the modelling perspective) between the scales at which herbivore and vegetation processes influence each other. Large herbivores influence vegetation proximately over very fine spatio-temporal scales, although ultimately their effects may become amplified over large areas and long time periods. Vegetation dynamics, however, directly influence large herbivores over a broad range of scales.

These issues are dealt with in the spatially explicit, process-oriented model of grassland, shrubland, savanna and forested ecosystems called SAVANNA. It is composed of a set of submodels which cover water balance, plant biomass production, plant population dynamics, litter decomposition and N cycling, ungulate herbivory, ungulate spatial distribution, ungulate energy balance and ungulate population dynamics. The model is described, and its strengths and weaknesses compared with the few other integrated models available.

Models which integrate large herbivore-vegetation processes at landscape scales have yielded high rewards both for increasing our level of scientific understanding, and have potential for allowing managers to evaluate potential outcomes of their decisions. However, if they are to serve a useful function for management, i.e. decision support systems, the models need to be accessible and transparent, and developed in interaction with stakeholders and end-users. Only then are managers likely to use the models appropriately, since the analysis and use of simulation results require knowledge about the inner workings of a model. None of the models currently available are decision support systems. Scientists need to go to greater lengths to make their models accessible if they are to be

useful for management decisions. Managers will need to become more willing to accept complexity and uncertainty, which is probably a good thing for nature!

In Chapter 13, **'Effects of large herbivores on other fauna'** by O. Suominen and K. Danell, considerable evidence is provided that large mammalian herbivores cause declines in the abundance of other herbivores feeding upon the same types of plants. This is particularly true for small mammals whose densities can be reduced by an order of magnitude. Since these are important prey for a large number of vertebrate predators, some of which are endangered species, the effects of large herbivores on the predator communities are potentially more important, from a conservation point-of-view, than the impacts of large herbivores on small mammals themselves. The application of the 'intermediate disturbance' hypothesis (i.e. that moderate grazing intensity maximizes animal diversity) is reviewed, and shown to be true in some, but not all circumstances, since some studies have found a monotonic relationship (usually negative impact of grazing intensity on diversity) (e.g. small mammals, passerine birds, terrestrial gastropods, web spiders).

The 'evolutionary history' of the community and the differences in the impacts of native vs. introduced large herbivores are shown to be important, so the predominantly negative effects of introduced browsers on invertebrate abundance and plant diversity in New Zealand habitats could be partly explained by the absence of large mammalian herbivores until recently.

One area of research which has been inadequately addressed so far is that other biota may have threshold densities of large herbivores to which they respond, so the choice of study systems in the past may have skewed the picture we have of how large herbivores shape community structures. 'Overgrazing' by large herbivores has been seen as an environmental problem, mainly because of their powerful effects on plants, but also on animal communities. However, in many wetlands and grasslands, grazing by large herbivores is used as a management tool for the conservation of birds, butterflies and other invertebrates. The impacts of grazing at different spatial and temporal scales have also been little studied, since most studies have been short-term explorations at the local scale. There is clearly a need for much more research, theoretical as well as applied, on the roles of large herbivores as modifiers of assemblages of other animals.

In Chapter 14, **'The future role of large carnivores in terrestrial trophic interactions: the northern temperate view'** by R. Andersen, J.D.C. Linnell

and E.J. Solberg, top-down and bottom-up views of population regulation in northern environments are reconciled, and the conditions under which herbivores can end up in a ‘predator-pit’ are explored. The authors show that the effect a large carnivore will have on a particular large herbivore population depends on (i) the presence of other predators, (ii) availability of alternative prey, (iii) the impact of food competition on the prey species, (iv) the degree of human harvest of both prey and predators, and (v) the mobility of the prey. The empirical evidence of the impact of predator control of northern boreal large herbivores leads to mixed conclusions, but it is widely recognized that most large carnivores are able to affect the abundance of their large herbivore prey strongly. The dichotomy of ‘top-down’ vs. ‘bottom-up’ regulation is too simplistic, and it is now widely accepted that it is the interaction of these processes that shapes the dynamics of herbivore populations.

A strong point of this chapter is that it shows that the subtle effects of a large carnivore on the behaviour of large herbivores can have strong effects on the use of resources, and on the population dynamics of the large herbivores. Because of fairly flat functional response curves (i.e. rapid increase up to a certain level) and strong human and intraspecific impact on large carnivore numerical responses, the impact of large carnivores will depend mainly on the large herbivore density. The authors conclude that the return of large carnivores to countries like Scotland/Germany (where roe deer, sika deer and red deer occur at very high densities) will do nothing to influence the dramatic impact of large herbivores on vegetation. Areas with mouflon and forest dwelling chamois could be an exception, where large carnivores like wolves and lynx could potentially exterminate mouflon and lead to marked changes in habitat use for chamois, from forest to mountain areas.

In multi-use landscapes it may be that large carnivores will have strong influences on large herbivore-habitat relationships locally, but weak effects regionally, because of the high densities (overabundance) of the large herbivores in these multi-use landscapes due to resource subsidies, management strategies of hunters etc. In contrast, in ‘natural’ systems or those with low productivity, large carnivores should limit ungulate population densities and therefore their impact on habitat. Humans now dominate both the top-down and bottom-up processes – often for the benefit of ungulates (at least in western Europe and North America). While fundamental research in ‘pristine’ areas is essential to allow basic ecological principles to be discovered, much more attention needs to be paid to multi-use landscapes, particularly long-term studies on trophic interactions and cascading effects in such systems. The authors conclude that ‘There are

today several studies in terrestrial ecosystems which indicate that the removal of large carnivores (and cessation of hunting by humans) have lead to dramatic increases in herbivore densities, which in turn have caused concern for long-term forest dynamics’.

The last two chapters of the book (Chapters 15 and 16) synthesizes the previous chapters. Chapter 15 describes the consequences for conservation of new insights in processes, and the very last chapter (16) highlights the general patterns which are emerging, generalizes our findings and identifies key areas for future research.

The previous chapters have shown how complex the large herbivore-vegetation interaction at the landscape scale can be, as it involves many different and interacting factors (e.g. plant competition, landscape pattern, climate, disturbance regimes and biogeochemical cycles). The earlier chapters demonstrate how difficult it is to find simple underlying principles. Simulation modelling has proved a useful tool for disentangling some of this complexity, and for integrating information across multiple scales. There are numerous modelling approaches, at varying levels of complexity which have been developed for different research objectives. Few models represent interactions between the two ecosystem components, animal and plant, in a balanced, integrated manner. Such integrated models include feedbacks and interactions between the components, typically including process-level representations for certain aspects of both plant and animal systems.

In Chapter 15, ‘**Restoring the functions of grazed ecosystems**’ by **I.J. Gordon**, shows how the new understanding of the ecological roles of large herbivores can be used to restore and/or maintain the functioning of ecosystems and the goods and services they provide is discussed. The concept of ecosystem health is defined, and the ways in which ecosystems can become degraded (i.e. lose the ability to provide the goods and services to humans) are reviewed. Two examples of using scientific information to manage ecosystems are presented, first, the restoration of hydrological function in degraded semi-arid savanna systems, secondly, the restoration of woodland in degraded Scottish forest.

In the savanna systems the main issue is that heavy grazing causes a decline in the proportion of precipitation which infiltrates the soil, leading to reduced plant productivity and resilience to perturbations, especially droughts. Intermediate grazing pressure can solve the problems, through a number of ecological mechanisms involving interactions between hydrology, plants and microorganisms in the soil. Financial analyses show that the reduction in grazing pressure need not be linked to financial losses.

The Caledonian forests have been reduced to 1% of their historical area, so successful management of the remaining ones is crucial to preserve several species of plants and animals which depend on this ecosystem. The main issue is the lack of regeneration of the ‘keystone species’ the Scots pine. Also research on the domestic and wild herbivores shows that regeneration can increase when browsing is reduced to intermediate levels. The intermediate grazing hypothesis is based on a spatial framework. Iain Gordon argues that this hypothesis should also be considered on a temporal basis, and it could be worth testing the idea that grazing systems and their herbivore populations should be managed not for stability, often at levels well below carrying capacity (as has often been the case in the past), but for temporal as well as spatial variability. Introducing temporal variability is more complicated, but could have important benefits for biodiversity conservation.

It is clear that managers cannot succeed in changing grazing practices without the consent of the people affected by these restoration efforts since people will be affected by many of the changes (in water quality, the number of animals available to hunt etc.). Iain Gordon concludes that ‘The future of many grazed ecosystems will depend upon scientists and practitioners forming a partnership in which scientists can investigate hypotheses at the landscape scale whilst managers can gain from the knowledge to provide guidance to management in the collaborative cycle for adaptive management.’

In Chapter 16, ‘Themes and future directions in herbivore-ecosystem interactions and conservation’ the editors identify four major themes or organizing principles which form a framework for understanding the richness of herbivore-ecosystem interactions described throughout this book. Two of these themes (body size and plant tissue chemistry) pertain to problems faced by large mammalian herbivores in securing enough resources to survive and reproduce in any ecosystem. The other two themes (the responses of individual plants to grazing or browsing and the alterations in plant and animal community composition) pertain to the effects of herbivores on ecosystems. Together, these themes could provide a framework for future directions in research in this area.

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Large herbivores across biomes

HERVÉ FRITZ AND ANNE LOISON

INTRODUCTION

The vertebrate herbivores cover a very wide range of body sizes from a few tens of grams to more than a tonne. It is therefore necessary to define what we consider as large herbivores: Bourlière (1975) described the bimodal distribution of mammal body weights and defined large mammals as being those with an adult body weight of more than 5 kg. A more recent analysis on a restricted set of species from Africa and America (Lovegrove & Haines 2004) also showed a bimodal distribution for herbivore body weights, with a gap slightly before 10 kg, separating most micro-herbivores (e.g. rodents, lagomorphs) from larger herbivores (mostly ungulates). Recently, however, large herbivores are often defined as those with body weight >2 kg (Ritchie & Olff 1999, Olff *et al.* 2002). We decided to keep the 2 kg threshold, which restricts large herbivores to mostly ungulates (*sensu lato*, i.e. Order Artiodactyla, Perissodactyla and including the Order Proboscidea) and to most herbivorous marsupials (*sensu* Fisher *et al.* 2001), all belonging to the Order Diprotodonta, and mainly to the Family Macropodidae. However we excluded from this synthesis the few large rodent species (e.g. capybara *Hydrochaeris hydrochaeris*) and the very large birds (e.g. ratites), which weigh over 2 kg. As it would take too long to show the patterns exhibited by ungulates as well as those from marsupials, we decided to comment on similarities and differences between these phylums, but to limit our main descriptions to ungulates.

With this definition in mind, we will describe patterns of species richness across a variety of biogeographical variables, such as continents,

climate and habitat types. We will concentrate on ungulate community structure and diversity, rather than on the determinants of abundance. The ungulate communities of African savannas are the only ones on which extensive work has been done regarding their overall abundance. The results show that their abundance seems to be determined primarily by the quantity, and possibly the quality, of the primary production, as the overall biomass of African savanna ungulates is positively related to annual rainfall and soil nutrient quality (Coe *et al.* 1976, Bell 1982, Fritz & Duncan 1994). This is consistent with the pattern found across biomes that secondary production is positively related to primary production (McNaughton *et al.* 1989). The determinants of the diversity of ungulates remain poorly understood, even in these well-studied and relatively intact communities. However, the interplay between the quantity and quality of primary production seems to drive the species richness of large herbivore communities, mainly through the trade-offs between digestive constraints and nutrient requirements, which are both primarily mediated by body size (Olf *et al.* 2002). The pattern described correctly fits the observed distribution, but the amount of unexplained variance calls for further investigations, including the implication of body size in interspecific competition and the role of other life history traits.

As diversity is the result of natural selection, which maximizes individual fitness through adjusting morphological, physiological, life history or behavioural traits to ecological conditions, we decided not to restrict ourselves to the description of taxonomic diversity, but also cover important traits. We have primarily used body size to describe diversity, as it is correlated with many morphological, physiological and life history attributes (e.g. Schmidt-Nielsen 1984, Gordon & Illius 1994). It also has the advantage of being available for a wide range of species, and has been the subject of analyses of basic spatio-temporal patterns (e.g. Rosenzweig 1995, Gaston & Blackburn 2000). Nonetheless, the debate on the mechanisms shaping the distribution of body sizes is still open (e.g. Kozłowski & Gawelczyk 2002). We used the recently published database on eutherian mammals (Ernest 2003) as the primary sources for this review (see Fisher *et al.* 2001 for a similar database on marsupials). In addition to body size, we have surveyed examples of the diversity of behavioural and life history traits in relation to ecological variables, in order to explore diversity with a broad life history strategy perspective. Our aim was to describe general patterns among ungulates and marsupials, and to discuss possible processes explaining these patterns at the scale of the continents, biomes and broad habitat types. Performing new comparative and multivariate

analyses was, however, beyond the scope of this review. From the 1990s onward (e.g. Felsenstein 1985, Harvey & Pagel 1991, Garland *et al.* 1992), most comparative studies of life history traits accounted for phylogenetic inertia to avoid spurious relationships due to non-independence between data measured on closely related species (Stearns 1992). We nevertheless also refer to studies performed before phylogenetic inertia became the rule, as not all analyses have been updated.

Large herbivores also have the advantage, as most large body size vertebrates, of having a relatively well-known palaeoecological history. We have tried to incorporate in this synthesis the many useful insights this provides into the diversity of large herbivores today (e.g. Vrba 1992).

DEFINITIONS OF BIOGEOGRAPHICAL AND BEHAVIOURAL CATEGORIES

A habitat is a place that contains the resources necessary for maintaining all the stages of the life cycle of an organism or species. Using correspondence analysis, Greenacre and Vrba (1984) showed that the gross vegetational physiognomy (i.e. the wood-to-grass ratio) is a good proxy for the habitat specificities of antelopes (Vrba 1992). This specificity allows the species to be classified into broad categories that describe the patterns of herbivore distribution and diversity. However, the continuum in vegetation physiognomy requires some categorization. We chose to use an existing definition of broad habitat (Janis 1988, Loison *et al.* 1999, Pérez-Barbería *et al.* 2001), and to follow an existing classification of species-habitat relationship (Van Wieren 1996), which is consistent with another independent compilation (Pérez-Barbería *et al.* 2001a), but with more species. We also use information in Walker's encyclopedia of mammals (Nowack 1991), and an International Union for the Conservation of Nature (IUCN) specialist group database, Vrba and Schaller (2000) and Strahan (1983) to complete the information when necessary.

Closed-habitat dwellers are defined as those species that spend most of the year in dense habitats (e.g. forests, woodlands, bushlands, thickets). Open-habitat species are those that predominantly use grasslands, whilst mixed-habitat dwellers are those species that use savanna, forest ecotone or both closed and open habitats depending upon the season or the population within a species. However, these habitats do not translate directly into biomes, so we have associated each species with a climatic zone to give an idea of the corresponding biome: mountain, grassland, temperate woodland, temperate forest, desert, savanna, wooded savanna or rainforest.

Feeding style is defined by the predominant type of plant material ($\geq 90\%$) in the year-round diet of the species (Janis 1988). Species whose diet is principally monocotyledons are classified as grazers; species with $\geq 90\%$ dicotyledons (i.e. tree and shrub foliage, including herbaceous dicotyledons, or fruit eaters) in their diet as browsers. Mixed-feeders are those species with 10%–90% grass in their diet. For habitats we used an existing classification (Van Wieren 1996, Pérez-Barbería *et al.* 2001), which we completed from the same sources as for feeding style. We acknowledge the fact that more information and a finer dietary classification are available for African bovids (e.g. Gagnon & Chew 2000), but we kept very broad classes to allow the comparison between continents, climatic zones and biomes.

Average group size are not available for all species, as only African ruminants have been subject to extensive reviews of the relationship between group size, body size and some life history traits (e.g. Jarman 1974, Brashares *et al.* 2000). Recent meta-analyses on marsupial life history traits provided sources of typical group size for the large herbivorous species (e.g. Fisher & Owens 2000, Fisher *et al.* 2001, 2002). As this set of group size data does not cover all the species, we classified species into group size categories, which were more widely available: (1) Solitary or in pair-living, (2) Family unit (2–4 individuals), (3) Small groups (5–9 individuals), (4) Medium groups (10–25 individuals), and (5) Large groups (>25 individuals). Ungulates are present in all categories, whereas marsupials cover classes 1 to 4, and most are in 1 to 3.

TAXONOMIC DIVERSITY

The herbivore group is very diverse across biomes and continents, but it is unevenly spread, with most species in the tropics. The number of extant ungulate species included in the taxonomic classification of Family is also very unevenly distributed (Table 1.1). Most ungulates are found in Africa, twice as many as in Asia, followed by Europe, South America and North America. The ungulate hot-spot in Asia is in the tropical south-east, and most of the species live in forests and dry woodlands. Overall, the latitudinal distribution of large herbivore taxa conforms to the decreasing gradient of diversity from the tropics to the poles found in most organisms (Rosenzweig 1995). Europe and Asia have, as could be expected, many species in common especially in the cold and temperate climatic zone of the Eurasian land mass. Europe and North America, and to a lesser extent northern Asia, also share species, mostly those having a circumpolar

Table 1.1. A summary of the distribution of 227 large herbivore species within each main Family, and between the main continents. Ungulate distributions follow the standard classification (e.g. Ernest 2003), with the recent update of the Artiodactyls (Vrba & Schaller 2000)

Order	Suborder	Family	No. Species	Africa	Europe	Asia	North America	South America
Proboscidea	Elephantoidae	Elephantidae	2	1		1		
Perissodactyla	Hippomorpha	Equidae	6	4	1	2f		
	Ceratomorpha	Tapiridae	4			1		3
Artiodactyla	Suina	Rhinocerotidae	5	2		3		
		Suidae	14	4	1	9f		
		Tayasuidae ^o	3					3
		Hippopotamidae	2	2				
		Camelidae	6	1f		2f		2
		Tragulidae	4					
	Ruminantia	Moschidae	6		3f	4f		
		Giraffidae	2	2				
		Antilocapridae	1				1	
		Cervidae	42*		7f	22f	6f	10
		Bovidae	130*	74	21f	36f	6f	

Note: f. Some species may be present on two continents; e.g. the wild horses, Wild boar, dromedary, Roe deer, Moose, Red deer, Reindeer, Muskox.

*Species with subspecies that are sometimes considered as possible species, e.g. Bontebok and Blesbok are considered only once.

^oTayasuidae are sometimes classified as Suidae.

distribution. Considerable movements occurred between the landmasses, especially between Eurasia and North America, and from Europe and Middle-East Asia to Africa, during the late Pliocene and Pleistocene time. In fact, most of the present day African Artiodactyls come from an influx of species from the Middle East (Colbert & Morales 1994). The difference in biodiversity between the Tropics and the temperate and cold zones could simply be due to the fact that the Tropics represent a much larger land area than any other climatic zone, as it is well known that diversity increases with area (Rosenzweig 1995). Diversity is also recognized to be increased by the productivity of ecosystems in conjunction with moderate levels of disturbance, which maintain the heterogeneity of habitats and presumably niches. In addition to the well-described latitudinal gradient in species diversity, there seems to be a longitudinal gradient in large herbivore species in the boreal zone, both in the Palearctic and Nearctic (Danell *et al.* 1996). Large herbivore diversity drops close to the Bering Strait and peaks in the interior of both landmasses, more weakly in the Palearctic. Interestingly, variables related to primary production (temperature, length of growing season) and habitat diversity (e.g. the number of tree species) influences species diversity in addition to the area of the boreal zone (Danell *et al.* 1996). This also suggests interplay between productivity, habitat diversity and herbivore diversity.

The classic humped-shaped relationship between primary production and species diversity has been found for East African ungulates (Western 1989) and more generally for East and Southern Africa (Fritz, unpublished 2003), with a recent study showing a log-normal shape (Ritchie & Olff 1999). This implies a maximum diversity at intermediate productivity, as is often found in studies of patterns in biodiversity (e.g. Rosenzweig 1995). As savannas are known to be subject to disturbances such as fire, it is possible that ungulate diversity is the result of the interaction between primary production and disturbance. However, Olff *et al.* (2002) demonstrated that the maximum diversity is found in sites with nutrient rich soils and intermediate productivity. Therefore there seems to be interplay between plant production and plant quality in limiting populations of ungulates of different sizes. These areas of high diversity in Africa correspond to open or wooded savannas in East and Southern Africa on volcanic soils (Olff *et al.* 2002). The prediction from their model seemed to fit reasonably well the predicted values from other hot-spots amongst the tropical climatic zone. However, there is a major difference between Africa and Asia for ungulates because it is in the tropical rainforests and woodlands that the highest diversity is found in Asia. This calls for

an investigation of the role of human pressure on ungulate diversity, as it is in a remote rainforest that the last ungulate species was discovered, in this otherwise very densely populated continent. It is worth noting that the distribution of species between Families and Orders has changed considerably in historical times. These historical constraints on existing species and body size ranges calls for a short summary of the recent theory on large herbivore palaeohistory and palaeoecology, in order to set the scene for the description and understanding of modern day patterns.

PALAEONTOLOGY

The evolution of mammals is remarkably well documented, as they are large enough to have left many fossils (Vrba 1992). From the earliest ungulates, *Protogulatum* in the late Cretaceous, to present day ruminants the history of large mammalian herbivores is punctuated with regular radiations and extinctions (e.g. Eisenberg 1981, Vrba 1987). After the rise of ungulates in the Paleocene and Eocene (60–30 million years BP), the large herbivore taxa were dominated by the Proboscideans, with the Mastodonts thriving on most continents in the Pleistocene (1–0.01 million years BP). Most of these ancestors to the present day elephants had disappeared by the end of the Pleistocene, as well as many large herbivores, under what is often considered as human overkill (Martin & Klein 1984): North America lost 79 large mammal species including 44 herbivores, South America lost 68 including 25 herbivores, and Eurasia lost 11 mammal species, most of them in Europe. The Perissodactyls radiated in the Tertiary, when they became the dominant ungulates in the world, with horses predominating in the Oligocene (30–20 million years BP) and Miocene (20–5 million years BP), together with rhinos in the Miocene. The extant (or living) representatives of these ancient herbivores persist only in the Tropics, except for the horses and asses which occur in temperate and arctic biomes. The Perissodactyls gave way to the Artiodactyls as the dominant herbivores during the Pleistocene, although primitive Artiodactyls were present in the Eocene (e.g. Eisenberg 1981). The Pleistocene was also marked by massive extinctions in Australia (43 herbivore species). In the process, the community of large herbivorous marsupials lost its very large species (e.g. the very large kangaroos *Macropus ferragus*, c. 150 kg), including megaherbivores such as the *Diprodon optatum* or *Zygomaturus trilobus* (Murray 1984).

Recent analyses of the palaeohistory of ungulates suggest that the massive change in the trophic structure and species diversity of ungulate

communities since the Miocene has been due to many factors (Janis *et al.* 2000, 2002, Cerling *et al.* 1997, 1998) in particular: the decline in atmospheric CO₂ that has slowly caused the reduction in abundance of C₃ plants in favour of C₄ plants that are less dependent on atmospheric CO₂; and an increase in temperature which has promoted arid climates over the globe, favouring more open habitats dominated by C₄ plants (Cerling *et al.* 1997, 1998). The main C₃/C₄ transition occurred sharply in the latest Miocene and early Pliocene (8–5 million years BP), and corresponded with a phase where open habitat ungulates (predominantly grazers) replaced those from more closed habitats (predominantly browsers). The observed changes in the structure and diversity of the ungulate community showed that grazers did not really replace browsers, but instead flourished after the rise of the mixed-feeders in the middle Miocene, when browsers were still numerous (Janis *et al.* 2000, 2002). The highest diversity of ungulates occurred in this period, all dietary types then decreased, in particular browsers, which were reduced by 80% in the Pleistocene. The fact that grazers and mixed-feeders became dominant is in agreement with the change in habitat structure. The change in the number of species strongly suggests that primary productivity of the planet also decreased severely in the last 14 million years BP or so (Janis *et al.* 2002), which is in agreement with the drop in atmospheric CO₂ from the middle Miocene with an accelerated decrease in the Pleistocene.

The gradual vegetation change, both in structure and in productivity, could be considered as an alternative non-exclusive hypothesis to the human overkill influence for the major Pleistocene extinctions in North America as well as in Europe (see Martin & Klein 1984). Recently Klein (2000) suggested that although humans have been eating ungulates for the last two million years, they might have had a dramatic impact only during the last glaciation (especially that of 11000 years ago) as many species or genera became extinct while they had survived previous glaciation/interglaciation events. Prior to 50000 years ago, and the advent of modern hunting techniques, human populations occurred at low densities, and their technologically primitive hunting methods were unlikely to have had a serious impact, so most extinctions before 50000 years ago were probably due to climatic/atmospheric changes. To conclude, if climate/vegetation changes may be considered as a likely explanation for changes in ungulate diversity and community structure from the Miocene to the early Pleistocene, most authors now concur that humans were the primary source of the rapid extinctions in the late Pleistocene, *c.* 10000 years BP (Smith *et al.* 2003). In Australia and New Guinea, the human

overkill phenomenon seemed to have occurred earlier, *c.* 45000 years BP (Smith *et al.* 2003, Johnson & Prideaux 2004). These very rapid changes in ungulate abundance and structure may also have had a more dramatic impact on the vegetation than the fairly gradual change started in the Miocene, which could question today the idea of what is considered as natural (Martin & Steadman 1999).

BODY SIZE, DIVERSITY AND DISTRIBUTION

Across the world, the distribution of ungulate body weight has a classic log-normal distribution (Fig. 1.1). The restricted range of body sizes in Australian marsupials does not allow for a comparison, but the level of diversity among marsupials is higher than the level of ungulate diversity in Europe, South and North America, where the range of their body size is comparable (Fig. 1.2). As expected from the taxonomic differences in diversity, Africa and Asia dominate the diversity of body sizes (Fig. 1.2), mostly because a large proportion occur in the tropical zone, which also contains a greater diversity of body sizes (Fig. 1.3).

There is much discussion about the reasons for the widespread, humped-shape distribution of body weights across taxa. The smaller number of large species is likely to be due to the fact that larger species face higher extinction rates and lower rates of evolutionary change (Fowler & MacMahon 1982, Vrba 1987). They also need more resources and more space, and hence live at lower densities than smaller species (Damuth 1981, Peters & Wassenberg 1983). The sharp decline in the number of small body sized species is less well understood: for ungulates there is a minimum size constraint for mammals which live exclusively on grass and browse (Van Soest 1994). Ungulates weighing less than 10 kg are forced to resort to frugivory or granivory, at least partly. However, the comparison between continents shows that it is not only the extreme range of sizes that make the difference in richness, but also a reduction in the number of medium sized species. This concurs with the information from palaeohistory, which suggests that medium sized herbivores, mostly browsers, disappeared in response to decreases in primary productivity in most ecosystems (see section above).

The nutritional explanation is the basis of a general conceptual model of large herbivore diversity (both in species number and body sizes), with primary production and soil fertility being the primary determinants of this diversity (Olf *et al.* 2002). The occurrence of larger herbivore species increases with plant moisture availability, almost independently of soil

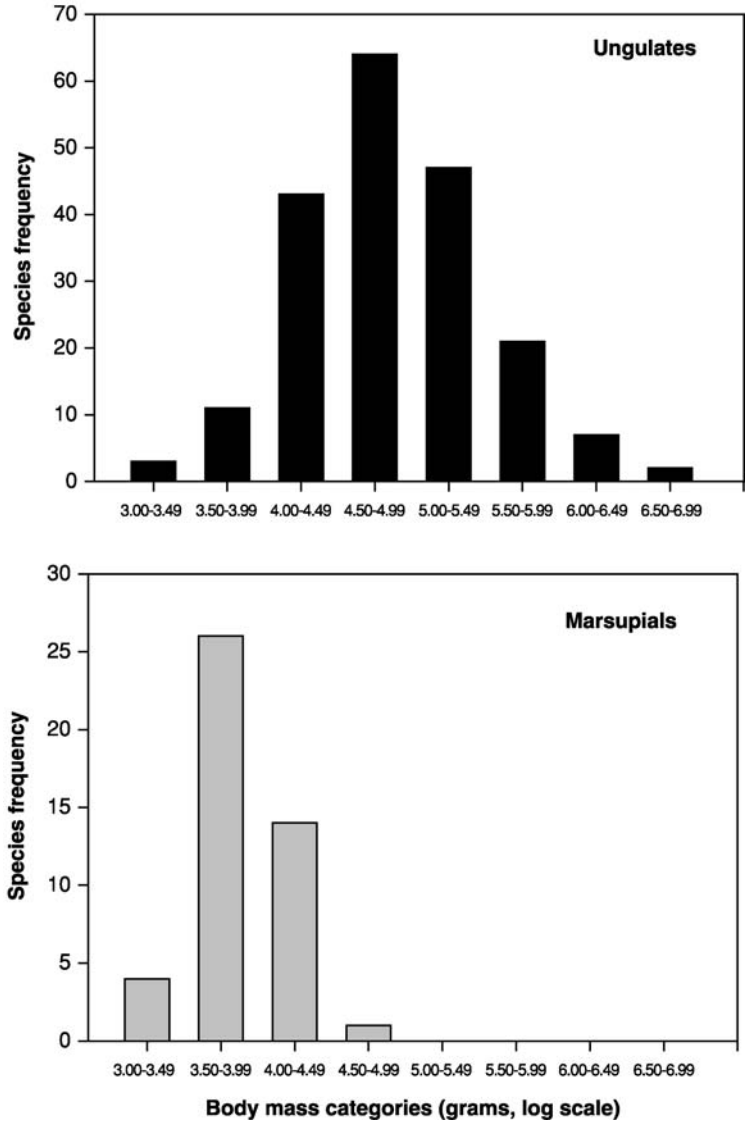


Figure 1.1. Distribution of body sizes in classes for the world ungulates and Australian herbivorous marsupials.

fertility, whereas small herbivores are mostly limited by soil fertility. Such patterns have been described in African savanna ungulate communities (Bell 1982, Fritz *et al.* 2002), for which the model was built originally, but the generality of this approach needs to be tested further. For instance, the

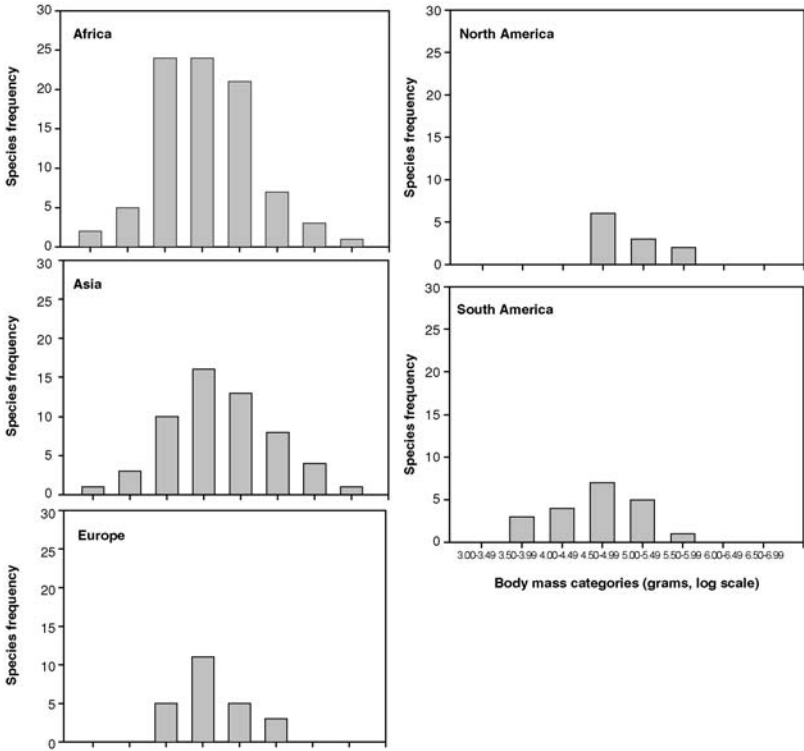


Figure 1.2. Distribution of native ungulate body sizes on the five main continents.

tropical rainforests with high moisture availability and, in general, low fertility are dominated by small species, when they should be dominated by megaherbivores (Fig. 1.4). The absence of these very large body sized herbivores may be due to extinctions, but the small number of medium sized ungulates is still puzzling. The relatively small number of species in the desert and mountain biomes, and their restricted body size range, is consistent with limitation by primary productivity, and with extra physiological constraints to cope with more extreme physical parameters. The savanna woodlands, and the temperate woodlands to a lesser extent, show a more uniform distribution of body masses than the more open or more forested biomes (Fig. 1.4). Interestingly, the distributions in body size show a tendency to be skewed to the right when compared in the broad habitat types (Fig. 1.5), with a wider range of species in less open habitat. The open habitat often comprised more seasonally stressed ecosystems,

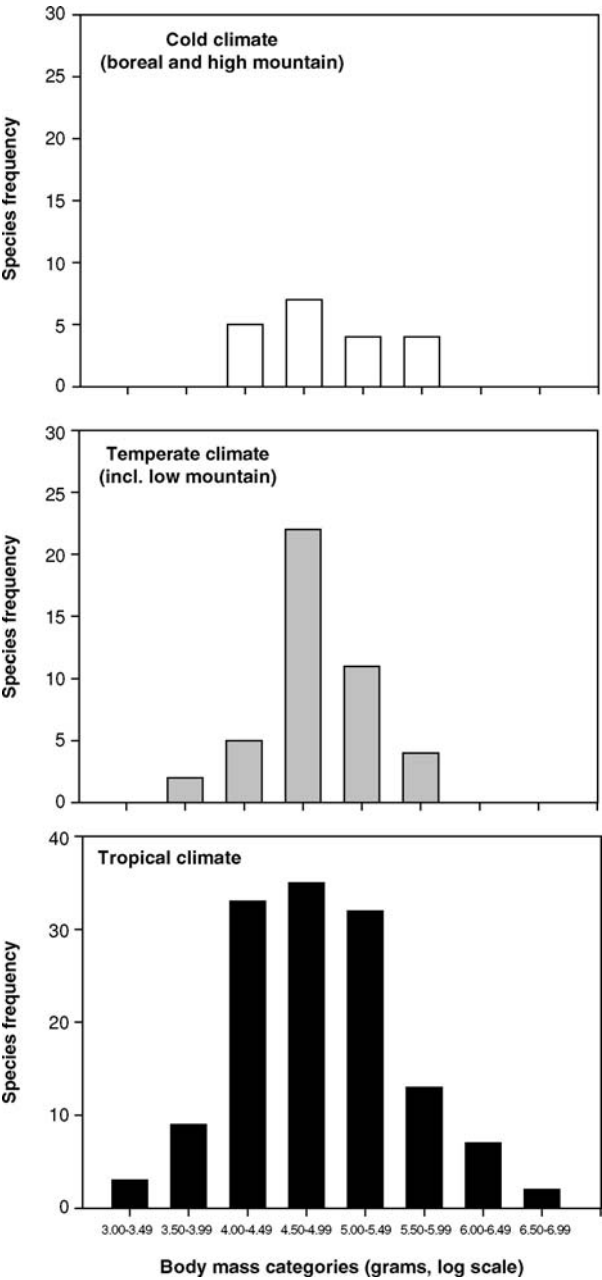


Figure 1.3. Body size distribution of ungulates per broad climatic region.

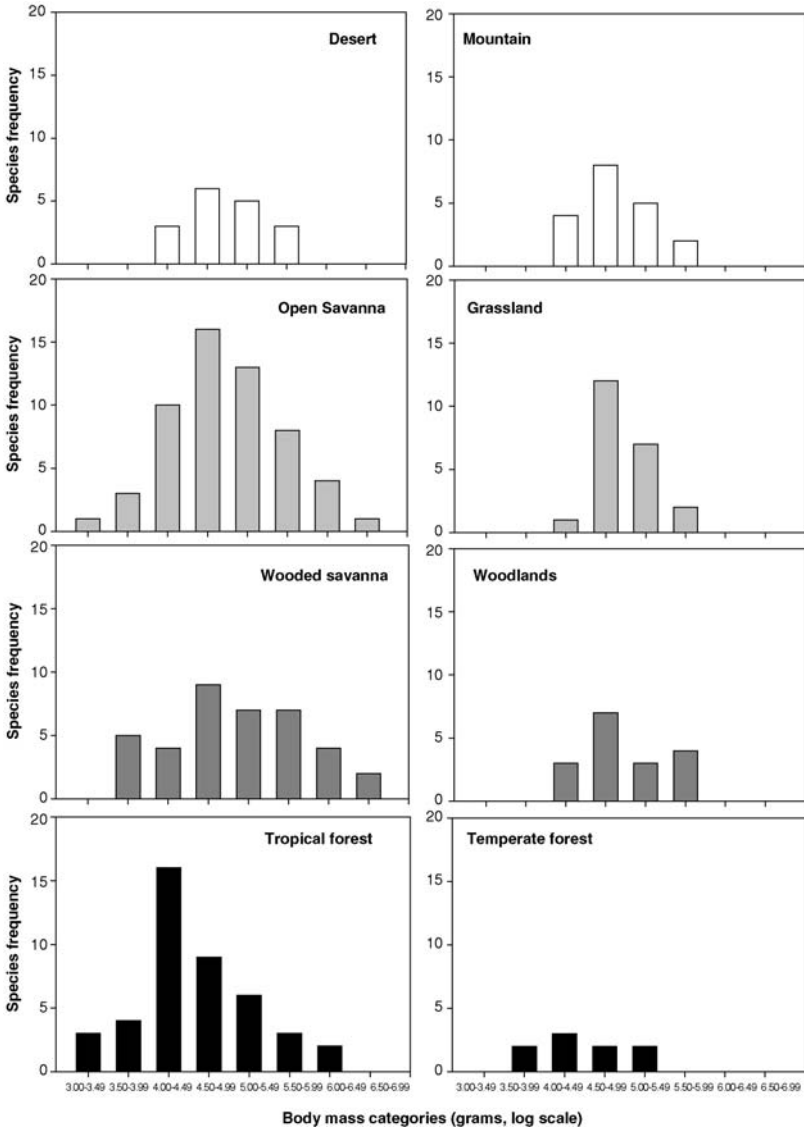


Figure 1.4. Body size distribution of ungulates in the main biomes (grassland and woodlands are the temperate equivalent of open savanna and wooded savanna in the Tropics).

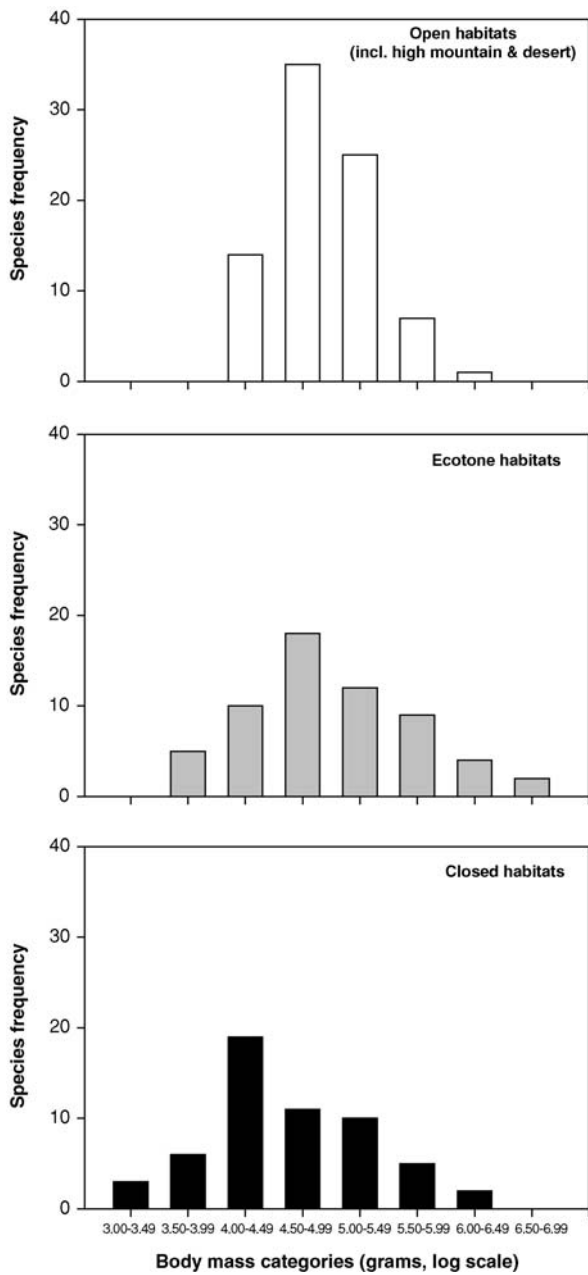


Figure 1.5. Body size distribution of ungulates in the main types of habitat.

which may result in greater constraints on the very large herbivores. Interestingly, the distribution of marsupials between the broad habitat types, does not match that of ungulates, as closed habitats have much greater diversity than open and ecotone habitats, but body size seems to increase slightly with habitat openness as in ungulates.

The different patterns between continents and biomes suggest that the feeding types of the herbivores may be important, as feeding types are likely not only to be correlated with habitat types, but also with the dynamics of their resources. For instance, browse resources are often less abundant and more heterogeneously distributed than grasses, and the relationship between the abundance of browse (shrubs or trees) and rainfall is not as simple as that for grasses, e.g. polynomial rather than linear (Lieth 1975, Deshmukh 1984, Le Houérou 1989). Consequently, the primary production structure and dynamics in different biomes and climatic zones is likely to affect feeding types differently.

GROUP SIZES AND FEEDING TYPES

The feeding types have different body weights, browsers being smaller than mixed-feeders, which are smaller than grazers, although there is considerable overlap in the range of body weights (Fig. 1.6). Interestingly, the largest ruminant is a browser. The distribution of body sizes within feeding types is slightly right-skewed, as in habitat types. This certainly reflects the link between habitat types and feeding types, but also suggests that the apparent log-normal distribution at the world level may in fact be the result of processes creating right-skewed distribution at the ecologically appropriate level of investigation. Although they have much in common, browsers and grazers may in fact differ sufficiently in the way they harvest food resources (e.g. review by Gordon 2003) to have different levels of constraints shaping their diversity.

Body size is perhaps more important in explaining differences in feeding types than morphological or physiological traits (Gordon & Illius 1994, Robbins *et al.* 1995, Pérez-Barbería & Gordon 1999). The ability to finely select plants and/or plant parts is associated with small muzzle size, which is strongly correlated to small body size. After controlling for phylogeny, only body size and two traits related to hypsodonty remained significant in the comparative analysis carried by Pérez-Barbería and Gordon (2001). Hypsodont (high-crowned) teeth in grazers are adapted to an abrasive diet, with high fibre, silicates and soil on the surface of leaves, i.e. plants growing in open areas. This suggests that the way food is

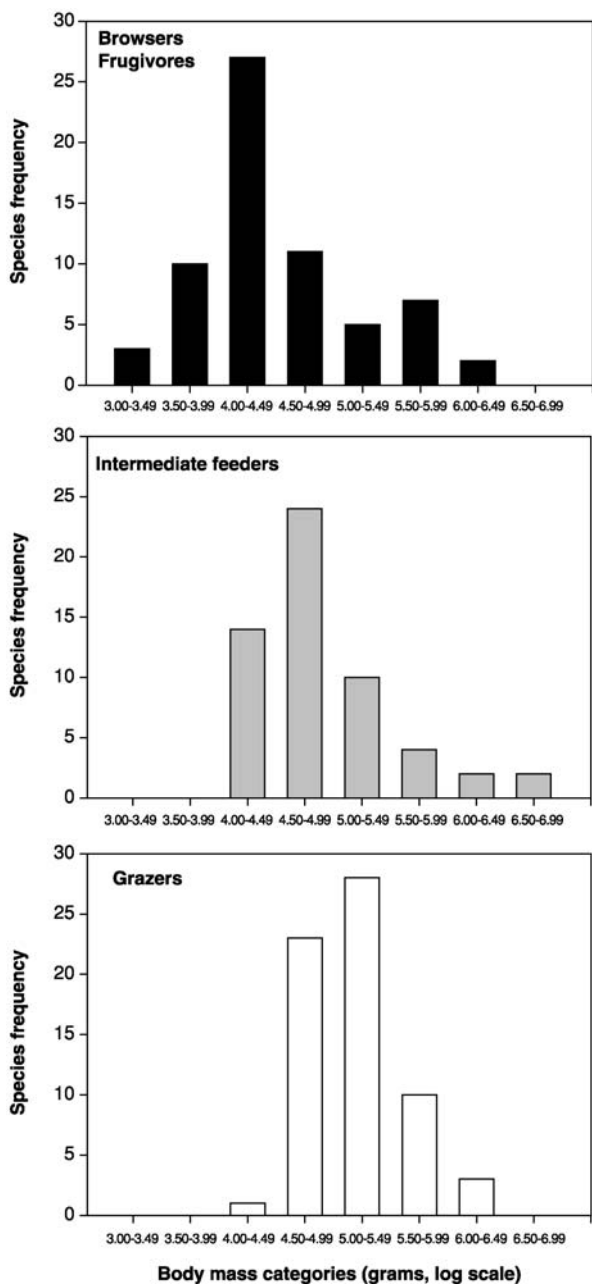


Figure 1.6. Body size distribution of ungulates in the main three feeding types.

processed in the mouth in relation to its structure (e.g. fibrousness) or composition (e.g. silicate) is more important in harvesting than mouth morphology. Low-crowned teeth are termed brachydont and correspond to a browse diet, medium-crowned teeth are termed mesodont and are those belonging to mixed-feeders (Janis *et al.* 2002). The hypsodonty index appears to be a good indicator of the broad feeding types, but also of the increase in abrasive particles in the diet within feeding types, i.e. a good indicator of the openness of the habitat: for instance the hypsodonty index increases from savanna to prairie in grazers, or from woodland to savanna for mixed-feeders (Janis *et al.* 2002). In a synthesis, Pérez-Barbería *et al.* (2001) proposed a scenario with a transition phase based on a diversification of mixed-feeder species both in closed and mixed habitat that lead to a multiplication of grazing species using mixed and open habitat. This is consistent with the reconstructed palaeohistory of dietary types (Janis *et al.* 2002) in which mesodonts (mostly mixed-feeders) flourished before hypsodont (grazers) started to diversify. It is also consistent with the relatively uniform distribution of body size in savanna woodlands and woodland, which are intermediate between forest and grassland dominated biomes, and hence have an intermediate structure (Fig. 1.4).

Since the seminal paper by Jarman (1974), it is known that ungulate feeding types, as well as other traits such as mating systems and predator avoidance, are associated with different group sizes. As group size is generally considered to be correlated with body size, this also reflects the correlation between feeding selectivity and body size, or between sexual dimorphism and body size (see sections below). Jarman's results and classification were revisited including a phylogenetic analysis, and although most of the relationships held qualitatively, there were large variations between Tribes (Brashares *et al.* 2000). Our descriptive approach to herbivore diversity exhibits some of these broad patterns. It appears that there are more solitary ungulate species at the small body size end of the spectrum, but the relationship is not striking (Fig. 1.7), and this pattern is not apparent in marsupials. The observed relationship between group size and habitat openness is more striking (Fig. 1.8), with species living in large groups being found primarily in open habitat. This is consistent with differences in anti-predator behaviour, the species in large groups in the open relying on vigilance and flight, whereas forest animals are hidiers (Jarman 1974, Brashares *et al.* 2000). The cost of vigilance for the individual is a strong evolutionary force to promote aggregation (Giraldeau & Caraco 2000). The pattern does not appear as clearly in marsupials. The relationship between group size and feeding types is consistent with the